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Journal

Ecosphere, 5(12)

ISSN

2150-8925

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Publication Date

2014-12-01

DOI

10.1890/es14-00173.1

Peer reviewed

Montane meadow hydrology, plant community, and herbivore dynamics

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Citation: Roche, L. M., A. T. O'Geen, A. M. Latimer, and D. J. Eastburn. 2014. Montane meadow hydrology, plant community, and herbivore dynamics. *Ecosphere* 5(12):150. <http://dx.doi.org/10.1890/ES14-00173.1>

Abstract. Montane meadows provide multiple ecological and economic benefits, and are widely considered areas of high conservation value. There is growing interest in balancing multiple land-uses on these and other focal working landscapes to provide for economic, social, and conservation goals. Globally, livestock grazing has been used as a management and conservation tool in many ecosystems; however, there is substantial concern—particularly for montane meadows—that grazing negatively impacts ecosystem functions and services. The mechanisms by which excessive livestock grazing can degrade meadow function have been well documented; yet, for hydrologically functional meadow systems, we know little about meadow-scale linkages in the hydrologic-soil-plant-grazing animal continuum, which limits our ability to develop riparian grazing conservation strategies. We conducted a cross-sectional, observational survey of hydrology, soils, plant communities, and cattle forage resource use across 24 functional montane meadows of the central Sierra Nevada Mountain Range in California, USA. By linking principles of plant community ecology and foraging theory, we were able to unravel relationships and drivers between hydropedologic conditions, plant community characteristics, and cattle grazing patterns. Our work demonstrates that hydrology is a critical driving factor of cattle foraging response, plant community attributes, and soil properties across these wetland ecosystems. Results indicate that these systems are resilient to the observed gradient of grazing disturbances. This information advances our understanding of how meadow-scale heterogeneity can be utilized in managing for multiple, and potentially conflicting, ecosystem services across working landscapes—particularly in the face of projected future climate changes and continually limited resources to support conservation and restoration projects.

Key words: Bayesian structural equation model; carbon sequestration; cattle; diversity; livestock grazing; mountain meadows; wetlands.

Received 19 June 2014; revised 15 September 2014; accepted 18 September 2014; **published** 16 December 2014.
Corresponding Editor: J. Nippert.

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INTRODUCTION

Globally, montane grasslands and wetlands deliver many ecosystem benefits to humankind. These diverse meadow systems provide flood water retention and sediment stabilization, maintain summer stream base flows, and support unique habitat and forage resources for pollina-

tors, wildlife, and domestic grazing animals (Hatfield and LeBuhn 2007, Roche et al. 2012, Acreman and Holden 2013). Meadows are important regional carbon and nitrogen sinks (Norton et al. 2011), and support species-rich plant communities distinct from the surrounding forest matrix (Allen-Diaz 1991, Kuhn et al. 2011). Balancing multiple—and potentially conflict-

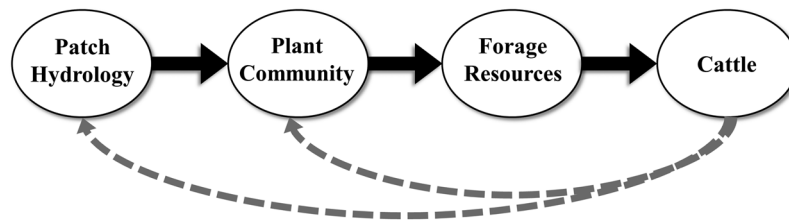


Fig. 1. Conceptual model of the hypothesized factors influencing patch-scale herbaceous forage utilization by cattle in montane meadows. Black arrows represent the specific hypotheses tested in this study; Grey arrows represent potential long-term feedback loops.

ing—economic, social, and conservation goals has become a central focus in the stewardship and conservation of these ecosystems.

Livestock grazing has been demonstrated to be a useful management tool for grasslands and meadows in some instances (Matejkova et al. 2003, Middleton et al. 2006, Rosenthal et al. 2012). However, in the western United States, many stakeholder groups have raised concerns about potential negative impacts of livestock on interdependent hydrologic, plant, and soil-based ecosystem services provided by mountain meadows (Fleischner 1994, Brunson and Steel 1996, Belsky et al. 1999)—this issue is notably controversial on publicly owned lands managed by the U.S. federal government. For wetland and riparian systems, it is well-established that excessive grazing and hoof compaction can negatively impact plant communities, hydrologic function, and resistance to soil erosion (Kauffman and Krueger 1984, Ratliff 1985, Fleischner 1994, Belsky et al. 1999, Flenniken et al. 2001, Toledo and Kauffman 2001, Cole et al. 2004). These impacts, in turn, can affect net primary productivity, nitrogen stocks, quantity and quality of soil carbon inputs, and organic matter decomposition (Blank et al. 2006, Pineiro et al. 2010, Norton et al. 2011). In a recent review, George et al. (2011) found strong evidence that riparian and wetland meadow resources can be protected through adaptive grazing management strategies—and potentially provide for multiple conservation and agricultural production outcomes.

In the Sierra Nevada Mountain Range in California, USA, meadows are part of a working landscape that is managed for multiple resource objectives, including cattle production, flow regulation, carbon and nitrogen sequestration,

and plant diversity. Despite the economic and ecological importance of these ecosystems, we know little about meadow-scale linkages in the overall hydrologic-soil-plant-herbivore continuum in this grazed landscape. Improved understanding of this continuum will enhance managers' abilities to forecast cattle grazing intensity patterns and spatially target meadow grazing strategies to balance multiple resource objectives. In this paper, we develop and test a comprehensive hydrologic-soil-plant-herbivore conceptual model characterizing the structure and drivers of this interdependent continuum (Fig. 1). Our conceptual model builds upon theory and research in both meadow plant community ecology—which centers on drivers of species diversity and plant community composition—and foraging behavior—which focuses on herbivore dietary selection patterns in a spatially diverse forage resource landscape.

High-elevation montane meadows exhibit considerable within-meadow variation in microtopography and water table dynamics, resulting in localized patches of distinct moisture regimes and associated plant communities (Allen-Diaz 1991). Research has clearly demonstrated that soil hydrology exerts strong controls on meadow plant community composition in these systems (Allen-Diaz 1991, Kluse and Allen-Diaz 2005, Loheide et al. 2009, McIlroy and Allen-Diaz 2012); that is, these local hydrologic regimes act as filters on the regional plant species pool (Weiher and Keddy 1995, Weiher and Keddy 1999, Casanova and Brock 2000). Herbivore foraging decisions are made at a hierarchy of ecological scales, spanning the home range (i.e., regional scale) to the small patch and individual bite locations (Senft et al. 1987, Bailey et al. 1996, Kie and Boroski 1996, Derner et al. 2012). Within

this hierarchy, animal behavioral patterns define scale boundaries: at the patch and bite scales, nutrient maximization and balance (e.g., forage quality in wetland meadows) drive diet selection, resulting in an overmatching of herbivore response to differentials in dietary rewards among units (Senft et al. 1987, Wallace and Crosthwaite 2005). Building on this knowledge, our conceptual model of meadow-scale hydrologic-soil-plant-foraging dynamics (Fig. 1) follows these premises: (1) patch-scale (i.e., within meadow) hydro-pedologic conditions (i.e., resulting from interactions between the pedosphere and hydrosphere) drive herbaceous plant community characteristics; (2) plant community characteristics determine available forage resource values (herbaceous forage quality and quantity) of patches; and (3) cattle grazing patterns (and thus patterns of intensity of environmental impact) are directly influenced by patch-scale forage resource variability.

In a two-step process to test the premises underlying our concept, we first broadly quantified relationships and drivers between patch-scale hydrology (shallow water table dynamics), plant community, and forage resource use by free ranging cattle across 24 hydrologically functional montane meadows in California's Sierra Nevada Mountain Range, USA. We then investigated connections and drivers between hydro-pedologic conditions (hydrology and soil indicators combined), plant community, and livestock grazing patterns across a subset of meadows via intensive soil sampling and analyses. We focused on hydrologically functional, long-term grazed meadows in order to examine these relationships under potentially sustainable riparian livestock grazing levels (i.e., levels that have not led to erosion or dewatering).

METHODS

Study area

This study was conducted across 24 meadows within the Sierra National Forest (SNF), on the western slope of the central Sierra Nevada in the upper montane zone. Study meadows spanned 2200 m to 2700 m in elevation and 0.3 ha to 7.9 ha in size. Thirty-year, 10-year, and 5-year mean annual precipitation for the study region was 125 cm, 115 cm, and 114 cm (PRISM 2014), respec-

tively, with the majority of precipitation falling as snow between December and April. The landscape is a mosaic of meadows, rock outcrops, and coniferous forests dominated by *Pinus contorta*, *Pinus jeffreyi*, *Abies concolor*, and *Abies magnifica*. Meadows in the region are characterized by shallow water tables (i.e., near-surface saturated conditions for at least part of the growing season), and are depositional zones with accumulations of stratified alluvial and organic materials. Soils display systematic variation resulting from saturation and sporadic deposition of fresh mineral sediment. Drier meadows and more well-drained meadow edges typically support Mollisols—mineral soils with high amounts of soil organic carbon. Poorly drained sites and locations with prolonged episodes of standing water tend to support Histosols—soils comprised predominantly of organic materials. Entisols and Inceptisols occur in zones of recently deposited mineral material (Wood 1975, Norton et al. 2011). Vegetation is characterized by a dense cover of largely perennial graminoid and herbaceous species. For the enrolled meadows, meadow-scale peak herbaceous biomass production ranged from 1000 to 3300 kg/ha (based on monitoring data from 2006–2008; Roche et al. 2012).

Grazing management

Like most mountain public grazing lands throughout the western United States, study allotments have been historically grazed by domestic livestock during the summer growing season. Study allotments ranged from 22,000 to 27,000 hectares, and were grazed by 200 to 235 permitted animal units (1 animal unit = 450 kg cow with or without nursing calf) per allotment between approximately 15 June and 20 September in the study year (range of 850 to 1080 animal unit months). Meadows were grazed by cattle under normal U.S. Forest Service allotment management, and were subject to annual grazing standards for (1) herbaceous vegetation use (remove no more than 35% of current year's forage production); (2) riparian woody plant use (remove no more than 20% of current year's leader growth); (3) streambank disturbance by livestock (no more than 10% of streambank physically damaged by hoof impact); and (4) streambank vegetation height (maintain a mini-

Table 1. Depth to low, mean, and high water tables for the driest (rank = 0), moderately wet (rank = 3), and wettest (rank = 6) calibration sites based on 2006, 2007, and 2008 monitoring data. Values are mean ± SE.

Wetness	Low (cm)	Mean (cm)	High (cm)
Driest	-67 ± 4.3	-45 ± 0.1	-21 ± 2.3
Moderately wet	-44 ± 7.3	-19 ± 3.4	-2 ± 0
Wettest	-4.8 ± 2.1	-1.0 ± 0.4	0 ± 0

mum of four inches) (Clary and Webster 1990, Hall and Bryant 1995, Clary and Leininger 2000, Freitas et al. 2014). For the enrolled meadows, average meadow-scale herbaceous forage use by cattle over three grazing seasons ranged from 0 to 50% (based on monitoring data from 2006–2008; Roche et al. 2012).

Sampling design and data collection

We conducted a cross-sectional, observational survey of plant communities, soils, and cattle forage resource use across 24 montane meadows during the 2007 summer growing season. Three to five sample sites (115 total sample sites) were established via a stratified random approach across each meadow catena (i.e., a toposequence reflecting effects of topography on proximity to water table and on water movement), representing existing dominant plant communities and moisture gradients (i.e., patches) across each meadow. Paired 1-m² plots (one plot open to grazing and one ungrazed caged plot) were randomly located within each plant community/moisture gradient sampling site. These sites served as the base sampling points for all data collection events.

Cattle utilization and vegetation attributes were recorded at each sampling site (n = 115). Cattle use was measured via total herbaceous vegetation consumed, which was determined via the comparative yield-paired plot method (Interagency 1996) at the end of the grazing period (mid-September). Peak herbaceous biomass production was measured at each 1 m² caged plot via the comparative yield method (Interagency 1996). During the peak production period, percent cover by plant species was determined via a 10 point frame, which was used to record 50 first-hit points (Bonham 1989, Interagency 1996).

Composite herbaceous forage samples were collected for each site in June, July, and August,

representing forage quality available during early, mid, and late growing seasons, respectively. For forage quality analyses, a minimum of 30 grams dry weight was sampled from each site, representing the local patch. Samples were oven-dried at 55–60°C for a minimum of 48 hours, and ground to pass through a 40-mesh screen. Crude protein (CP), acid detergent fiber (ADF), and total phosphorous (TP) were determined for each sample by the University of California Agriculture and Natural Resources Analytical Laboratory, UC Davis, California. CP was directly calculated from sample nitrogen content, which was measured via nitrogen gas analyzer utilizing induction furnace and thermal conductivity (AOAC 2006). ADF was determined gravimetrically as the residue remaining after acid detergent extraction (AOAC 1997a). For TP, samples were processed via nitric acid/hydrogen peroxide microwave digestion; TP was quantitatively determined by inductively coupled plasma atomic emission spectrometry (Meyer and Keliher 1992, Sah and Miller 1992). Given that plant nutritional quality declines with maturity—and the magnitude of these declines vary with site conditions (e.g., wet versus dry sites)—we used a seasonal average (i.e., averaged over early, mid, and late growing seasons) of each metric to better capture the forage quality profile across the grazing season.

A meadow patch hydrologic rating scale was previously developed and calibrated at 31 sites within 10 study meadows equipped with ground water wells and monitored intensively throughout three years, 2006 through 2008 (see McIlroy and Allen-Diaz 2012, and Roche et al. 2012 for data and analyses). All 115 sample sites in this study were categorized along this relative wetness scale with scores ranging from 0 to 6, as integers (Roche et al. 2012). Sites were rated based on extent and timing of surface flooding and saturation, dominant plant functional groups (e.g., wetland obligates), and hydric soil indicators (mineral vs. organic layers, depth of peat accumulation in organic soils, and abundance of redox concentrations and depletions in mineral soils). Patch hydrologic ratings (i.e., patch wetness) reflected seasonal water table variation between the driest, moderately wet, and wettest rated sites in meadows equipped with ground water wells (Table 1).

Thirty-six sample sites across nine representative meadows were selected for intensive soil profile descriptions, and soil sample collection and analysis. These thirty-six sample sites and nine meadows were representative of the larger sample set (115 sites, 24 meadows), ranging from relatively drier (i.e., seasonally wet) to wet (i.e., standing water present throughout entire season) conditions. A total of 36 soil profiles were excavated at three to five sampling sites per each of the nine meadows to characterize soil morphological, physical, and chemical properties to 50 cm depths. For mineral soil layers, bulk density samples were extracted via the core method (Blake and Hartage 1986). For organic soil layers, blocks approximately 1000 cm³ were extracted and dimensions recorded. All bulk density samples were dried to constant weight at 105°C.

Soil samples were collected from each genetic horizon for soil characterization and analyses. Percent organic matter was determined by loss on ignition (Nelson and Sommers 1996), and degree of decomposition for organic horizons was determined via rubbed fiber content and pyrophosphate color methods (Soil Survey Staff 2006). Soil pH was analyzed in 1:1 soil/water suspensions after 30-minute equilibration (Thomas 1996). Total soil organic C (SOC) and total N (TN) were determined by dry combustion of oven dried (65°C for 24 hours), powdered samples using a Carlo Erba NC-2100 elemental analyzer (Carlo Erba Instruments, Milan, Italy [AOAC 1997b]). TC, TN, and SOC were summarized as 50 cm depth-weighted averages.

Data analyses

Data analysis was conducted in two stages. First, based on the broader dataset of 24 meadows, we assessed relational pathways between patch-scale (within-meadow) hydrology, plant community characteristics, and cattle forage resource use. We then focused on the nine intensively sampled meadows to posit relational pathways between hydro-pedologic conditions (hydrology and soil), plant community characteristics, and cattle foraging patterns across meadow catenas. For both datasets, we first examined simple bivariate relationships and then utilized Bayesian structural equation modeling (SEM) to test hypothesized relational pathways.

Bayesian SEM is a flexible, multivariate analysis technique combining both path and factor analyses to provide greater systems-scale understanding than more traditional approaches (Bollen 1989, Congdon 2003, Grace 2006, Lee 2007, Roche et al. 2012).

Patch hydrology, plant community, and cattle foraging dynamics.—We used linear mixed effects models to examine bivariate relationships between patch hydrology and plant community attributes (diversity, forage quality, productivity), and cattle grazing. Given the widespread emphasis on biodiversity conservation and management on grazed wetlands (e.g., Matejkova et al. 2003, Middleton et al. 2006, Symstad and Jonas 2011), we also examined the relationship between patch-scale plant species diversity and herbaceous utilization by cattle. Diversity (Shannon-Wiener Index), richness, and evenness were calculated in PC-ORD version 5.10 (McCune and Grace 2002). Linear mixed effects model analyses were conducted in STATA (StataCorp 2013). Data were hierarchically structured with sample sites nested within-meadows; to account for potential non-independence due to this structure, meadow identity was included as a random effect (i.e., random intercept) (Pinheiro and Bates 2000, Rabe-Hesketh and Skrondal 2008). Bivariate regressions were fit with linear and quadratic functions, and AIC and significance tests were used to select final models (Pinheiro and Bates 2000, Rabe-Hesketh and Skrondal 2008). Standard diagnostic analyses were utilized to check distributional assumptions and constant variance, and transformations and/or variance functions were used to remedy any violations (StataCorp 2013). Traditional R^2 values are invalid for mixed effects models; therefore, to generally assess model fits, pseudo- R^2 values were calculated from linear regressions between observed and predicted values. Predicted values were obtained based on both fixed and random effects (as a metric of overall model fit) and for fixed effects only (to reflect how much variance the fixed effects explained) (Tate et al. 2003, Gabriel et al. 2010).

We used Bayesian structural equation modeling (SEM) to examine relational pathways between patch hydrology, plant community diversity components (richness and evenness), forage resources, and cattle utilization (Fig. 1).

Bayesian SEM analysis was performed via OpenBUGS software, which uses Markov chain Monte Carlo (MCMC) simulation based on a Gibbs sampling algorithm to fit models (Thomas et al. 2006). Variables with non-normal distributions were transformed to meet distribution assumptions, and standardized regression coefficients were reported. To account for non-independence of sample sites, meadow identity was included as a random effect (Pinheiro and Bates 2000, Gelman and Hill 2007, Rabe-Hesketh and Skrondal 2008). Model convergence was assessed utilizing trace plots with multiple chain sample values and a modified Gelman-Rubin statistic (Spiegelhalter et al. 2007). Model comparisons and goodness of fit were assessed via the Deviance Information Criterion (DIC), a generalization of Akaike's Information Criterion (AIC) (Spiegelhalter et al. 2002). Reliability of model coefficients was examined via credible intervals (i.e., Bayesian equivalent of confidence intervals).

Hydropedologic conditions, plant community, and cattle foraging patterns.—We used three representative profiles (driest, moderately wet, and wettest patches) from the nine intensively sampled meadows to graphically summarize common trends in morphological, physical, and chemical soil properties. Linear mixed effects analyses were utilized to examine bivariate relationships of (1) TN, SOC, and SOM by patch hydrology; (2) TN and SOC by forage quality (seasonal averages of TP, CP, and ADF); (3) TN, SOC, and SOM by cattle forage utilization; and (4) surface soil bulk density by cattle forage utilization. For analyses of TN, SOC, and SOM by cattle utilization, we included a grazing by patch hydrology interaction term to account for potential differences in cattle grazing effects across patch wetness types. For analysis of surface soil bulk density by cattle utilization, we examined both the main effect of grazing and a grazing by SOM interaction term—to account for potential differences in inherent site resiliency (i.e., to compaction disturbances by cattle) due to differing SOM contents across sites. Linear mixed effects analyses followed the same methodology as described above.

Following simple bivariate analyses, we used Bayesian SEM to test relational pathways between hydropedologic conditions, herbaceous plant community, and cattle foraging patterns.

The Bayesian SEM analysis followed the same methodology as described above.

RESULTS

Patch hydrology, plant community, and cattle foraging dynamics

Linear mixed effects regression analysis revealed significant bivariate relationships between the measured plant community characteristics and patch hydrologic rating (0–6, with 6 representing the wettest rating). Forage quality (Fig. 2A–C) and plant community diversity (Fig. 2D) were negatively related ($p < 0.01$) to hydrologic rating (i.e., patch wetness); however, peak herbaceous biomass production was not significantly ($p > 0.10$) related to hydrologic rating. Herbaceous forage utilization by cattle was negatively related ($p < 0.0001$) to hydrologic rating (Fig. 3A) and positively related ($p < 0.0001$) to plant community diversity (Fig. 3B). While herbaceous forage utilization at the patch-scale was more than 50% for many sites (Fig. 3), average use across all meadows during the 2007 study period (28%) was below USFS annual vegetation use standards (35%). The most diverse sites (upper 10th percentile) were co-dominated by multiple forbs (e.g., *Phalacroseris bolanderi*, *Polygonum bistortoides*, and *Mimulus* spp.), sedges (e.g., *Carex jonesii*, *Eleocharis* spp.), rushes (*Juncus oxymeris*), and grasses (*Agrostis* spp., *Deschampsia caespitosa*). Sample sites in the lowest 10th percentile for diversity were largely dominated by *Carex utriculata*, *Eleocharis* spp., and *Carex simulata*.

Bayesian SEM results revealed relationships between patch hydrologic rating, forage quality, herbaceous forage production, and forage utilization by cattle (Fig. 4), supporting our conceptual model. Patch hydrology negatively influenced local patch-scale community diversity (wetter patches exhibited significantly lower diversity), and diversity positively influenced overall forage resource value (herbaceous forage quality and quantity). Livestock utilization positively responded to local patch-scale forage resources, with the individual forage quality metrics exhibiting relatively greater importance than forage quantity (forage quality indicator coefficients were an order of magnitude greater than the forage production coefficient; Fig. 4).

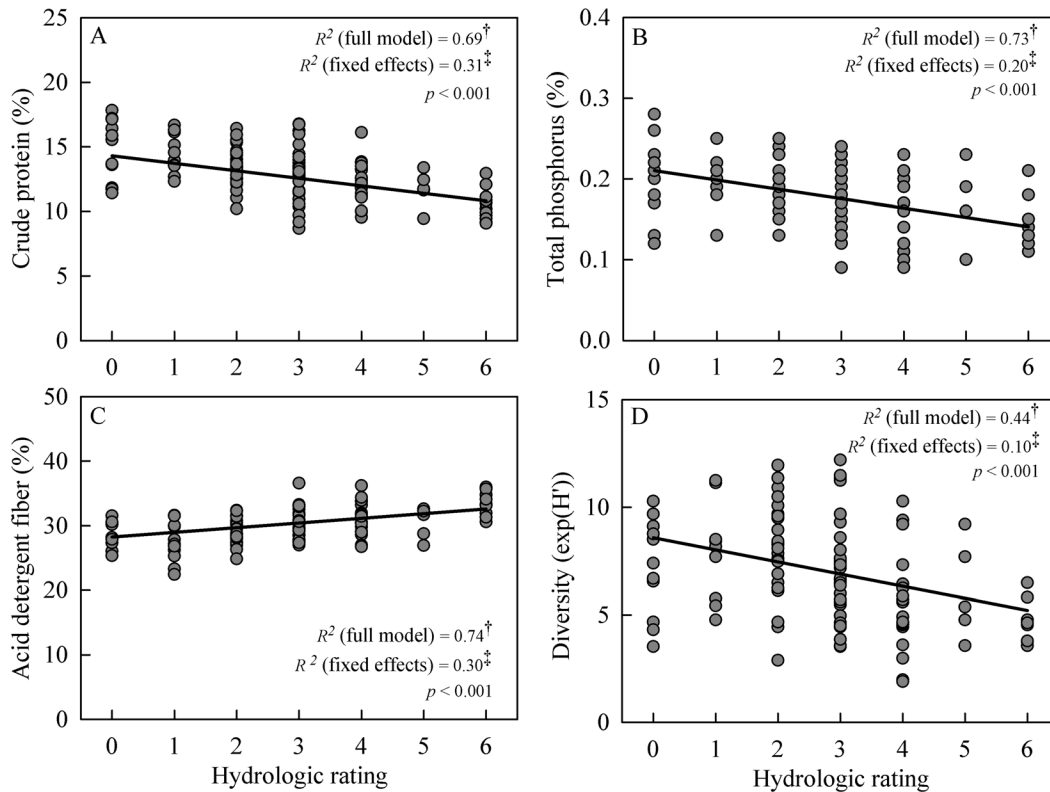


Fig. 2. Forage quality (crude protein, total phosphorus, and acid detergent fiber; A–C) and plant community diversity (D) responses to patch hydrologic rating (0 = driest and 6 = wettest). Shannon-Wiener Index (H') is converted to the effective number of species by taking the exponential. The p -values are from linear mixed effects model results (i.e., Wald test of fixed regression coefficient). A dagger (\dagger) indicates pseudo- R^2 values calculated from linear regression between observed and predicted values with predictions based on fixed and random effects; a double dagger (\ddagger) indicates pseudo- R^2 values calculated from linear regression between observed and predicted values with predictions based on fixed effects only (cf. Tate et al. 2003, Gabriel et al. 2010).

Hydropedologic conditions, plant community, and cattle grazing patterns

The driest sample sites were dominated by mineral horizons, with highly decomposed organic horizons present in some cases. Moderately wet patches were dominated by organic horizons with both moderately and highly decomposed organic materials. Surface soil horizons in the wettest patches were dominated by slightly to moderately decomposed organic materials, with highly decomposed residues dominating underlying horizons (Fig. 5). SOC, TN, and SOM generally increased with patch wetness, with the greatest differences between the driest and wettest patches (Table 2). Approximately 40% of soil profiles sampled had either buried horizons or sand lenses present, indicating

substantial, episodic depositional events from surrounding uplands.

We found significant second-order polynomial relationships for 50-cm depth-weighted average SOC, TN, and SOM by patch hydrologic rating (Fig. 6). SOC and TN were also significantly ($p < 0.005$) related to average grazing season values for the forage quality metrics; lower forage quality (i.e., low CP and TP, and high ADF) values were associated with greater soil TN (Fig. 7A–C) and SOC (Fig. 7D–F). Neither the main effect of grazing nor the grazing by patch hydrology interaction term were significant predictors for TN, SOC, or SOM (all significance values > 0.1 ; Fig. 8A–B, data for SOM not shown). Additionally, neither the main effect of grazing nor the grazing by SOM interaction term

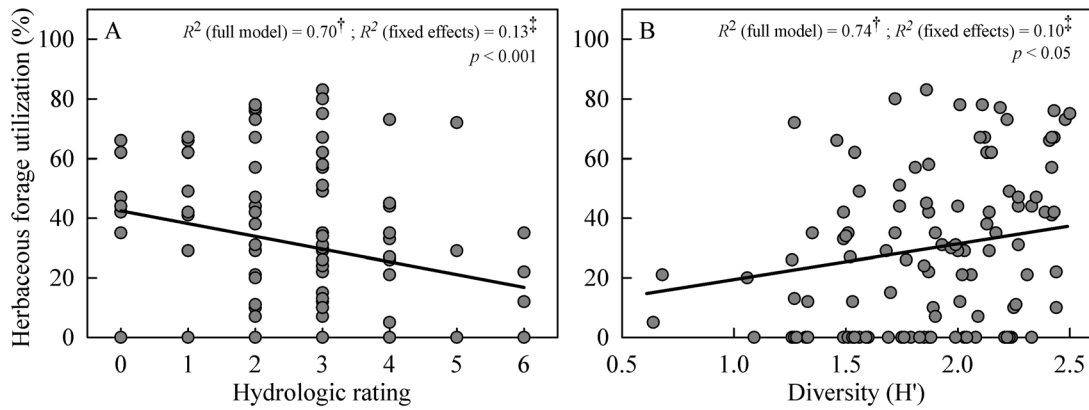


Fig. 3. Percent herbaceous forage utilization by cattle was negatively correlated with (A) patch hydrologic rating (0 = driest and 6 = wettest) and positively correlated with (B) plant community diversity. The *p*-values are from linear mixed effects model results (i.e., Wald test of fixed regression coefficient). A dagger (†) indicates pseudo-*R*² values calculated from linear regression between observed and predicted values with predictions based on fixed and random effects; a double dagger (‡) indicates pseudo-*R*² values calculated from linear regression between observed and predicted values with predictions based on fixed effects only (cf. Tate et al. 2003, Gabriel et al. 2010).

were significant (*p* > 0.1) predictors for soil surface bulk density (Fig. 8C).

Bayesian SEM results revealed relational pathways between hydropedologic conditions, herbaceous plant community, and cattle resource use patterns across meadow catenas. The herbaceous plant community (with diversity and forage quality indicators showing the highest importance values; Fig. 9) was negatively influenced by hydropedologic conditions—wetter sites with greater SOM, TN, and TC stocks exhibited lower diversity and forage quality. Similar to analysis of the larger meadow dataset, cattle grazing positively responded to the patch-

scale herbaceous community, with forage quality and diversity indicators exhibiting relatively greater influence than forage quantity (Fig. 9).

DISCUSSION

At the landscape scale, cattle are known to preferentially select meadow and riparian habitats within a forested matrix (Kie and Boroski 1996), and specifically select for relatively drier (i.e., mesic) meadows with greater herbaceous forage resource values (Roche et al. 2012). Both bivariate and Bayesian SEM analyses revealed that—at the patch scale of decision-making—

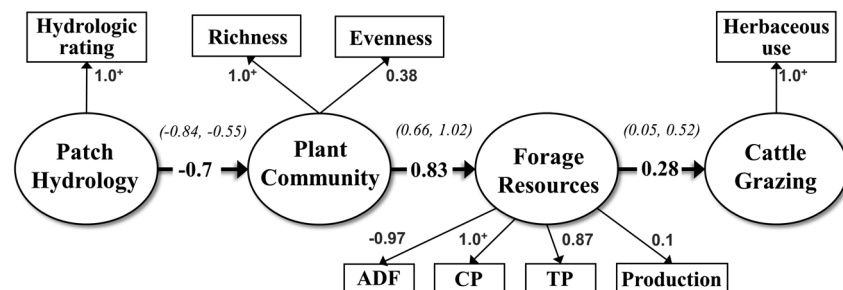


Fig. 4. Results for Bayesian structural equation modeling of patch-scale hydrology, plant community, and cattle foraging dynamics. Ovals indicate latent variables, which are estimated by observable indicators, represented by boxes. A plus sign indicates a fixed value. Values in parentheses are 90% Bayesian credible intervals.

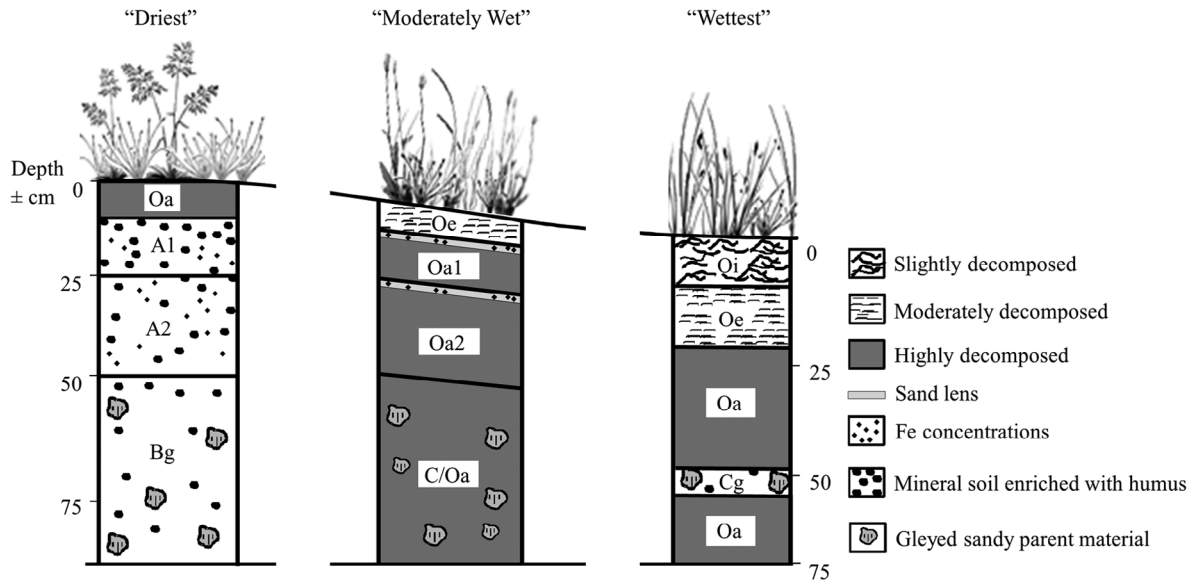


Fig. 5. Morphologic properties and associated stratigraphy of representative patches across all sampled meadows. Stratigraphy is based on one representative profile from each hydrologic rating (driest = 0 rank, moderately wet = 3 rank, and wettest = 6 rank). See Table 2 for physical and chemical properties.

cattle select relatively drier sites (Fig. 3A) which have greater forage resource values and greater plant species diversity (Figs. 2, 3B, and 4). The

more diverse patches also likely enable cattle to select for a mixed diet, which has been demonstrated to be a major determinant in dietary

Table 2. Physical and chemical properties of representative patches (driest = 0 rank, moderately wet = 3 rank, and wettest = 6 rank) across all sampled meadows. Values are means \pm SE ($n = 3$ for driest patches, $n = 4$ for both moderately wet and wettest patches). See Fig. 5 for morphologic properties and associated stratigraphy.

Depth (cm)	SOC (g/kg)	Total N (g/kg)	SOM (g/kg)	Bulk density (g/cm ³)
Driest (Mesic)				
0–5	104 \pm 19	7.5 \pm 1.2	218 \pm 37	0.59 \pm 0.14
5–10	77 \pm 20	5.8 \pm 1.3	165 \pm 40	0.69 \pm 0.20
10–20	47 \pm 6.1	4.0 \pm 0.5	98 \pm 5	1.00 \pm 0.06
20–25	44 \pm 7.8	3.7 \pm 0.7	92 \pm 9	0.99 \pm 0.08
25–50	19 \pm 4.1	1.7 \pm 0.4	62 \pm 14	0.95 \pm 0.09
Moderately wet				
0–5	294 \pm 51	16.0 \pm 2.3	606 \pm 90	0.16 \pm 0.03
5–10	241 \pm 47	15.1 \pm 2.8	447 \pm 83	0.33 \pm 0.10
10–15	183 \pm 39	13.0 \pm 2.9	312 \pm 47	0.50 \pm 0.07
15–20	179 \pm 42	11.9 \pm 2.6	402 \pm 109	0.47 \pm 0.09
20–25	192 \pm 51	13.1 \pm 3.1	452 \pm 112	0.41 \pm 0.08
25–40	196 \pm 49	14.0 \pm 3.0	474 \pm 104	0.37 \pm 0.07
40–45	202 \pm 49	14.4 \pm 2.8	491 \pm 100	0.36 \pm 0.07
45–50	233 \pm 43	16.9 \pm 1.6	579 \pm 56	0.29 \pm 0.01
Wettest				
0–5	291 \pm 66	13.1 \pm 2.6	617 \pm 125	0.14 \pm 0.06
5–10	288 \pm 65	13.2 \pm 2.6	608 \pm 122	0.14 \pm 0.06
10–15	234 \pm 77	11.1 \pm 3.6	449 \pm 154	0.38 \pm 0.19
15–20	204 \pm 80	11.3 \pm 4.5	355 \pm 140	0.45 \pm 0.18
20–25	183 \pm 71	11.4 \pm 4.6	245 \pm 101	0.50 \pm 0.15
25–30	193 \pm 67	12.2 \pm 4.3	252 \pm 98	0.47 \pm 0.15
30–35	193 \pm 67	12.6 \pm 4.1	254 \pm 98	0.57 \pm 0.25
35–45	129 \pm 44	9.01 \pm 2.9	179 \pm 41	0.66 \pm 0.22
45–50	122 \pm 42	8.53 \pm 2.8	175 \pm 41	0.68 \pm 0.22

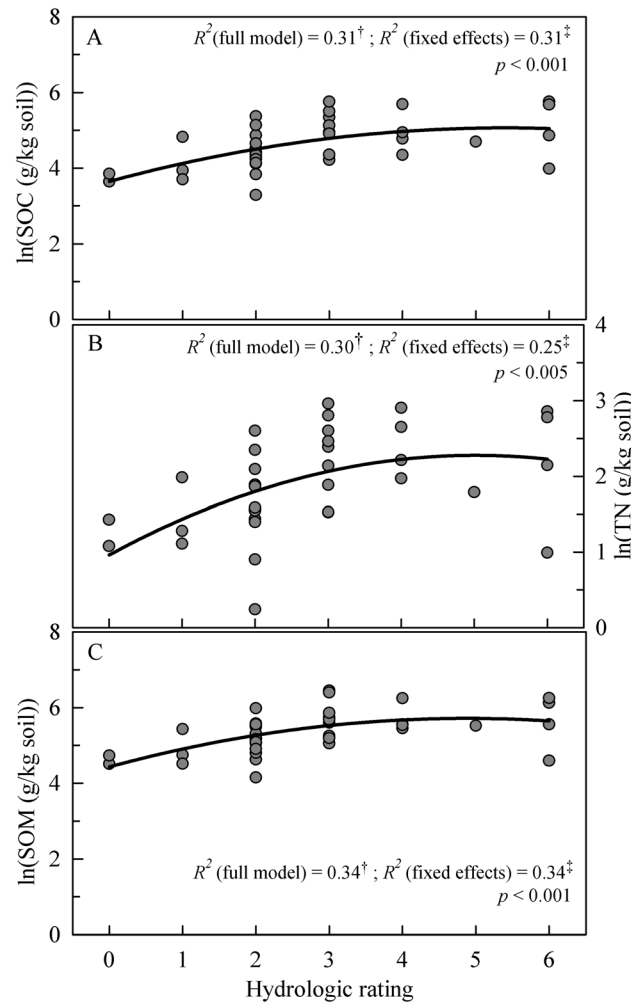


Fig. 6. Relationships between patch hydrologic rating (0 = driest and 6 = wettest) and (A) total soil organic carbon (SOC); (B) total nitrogen (TN); and (C) soil organic matter (SOM). All values are ln(50-cm depth-weighted averages). The *p*-values are from linear mixed effects model results (i.e., Wald test of fixed regression coefficient); a dagger (†) indicates pseudo-*R*² values calculated from linear regression between observed and predicted values with predictions based on fixed and random effects; a double dagger (‡) indicates pseudo-*R*² values calculated from linear regression between observed and predicted values with predictions based on fixed effects only (cf. Tate et al. 2003, Gabriel et al. 2010).

selection by grazers (Soder et al. 2007). Overall forage resource value was determined to a greater extent by forage quality metrics than by forage productivity (Figs. 4 and 9); previous work in foraging theory on drivers of herbivore selectivity has also demonstrated that patch selection is largely based on diet quality (WallisDeVries et al. 1998, 1999).

Meadow soil characteristics were largely driven by hydrologic controls rather than grazing

disturbances across these wetland systems. The measured soil properties significantly responded to patch-scale hydrologic variation; the wetter patch types, produced by season-long high water tables, had the greatest accumulations of SOC, TN, and SOM (Fig. 5 and Table 2). Extended periods of saturation and inundation at wetter patch types slows organic matter decomposition, due to anoxic conditions driving use of the less efficient microbial energetic pathways, thus

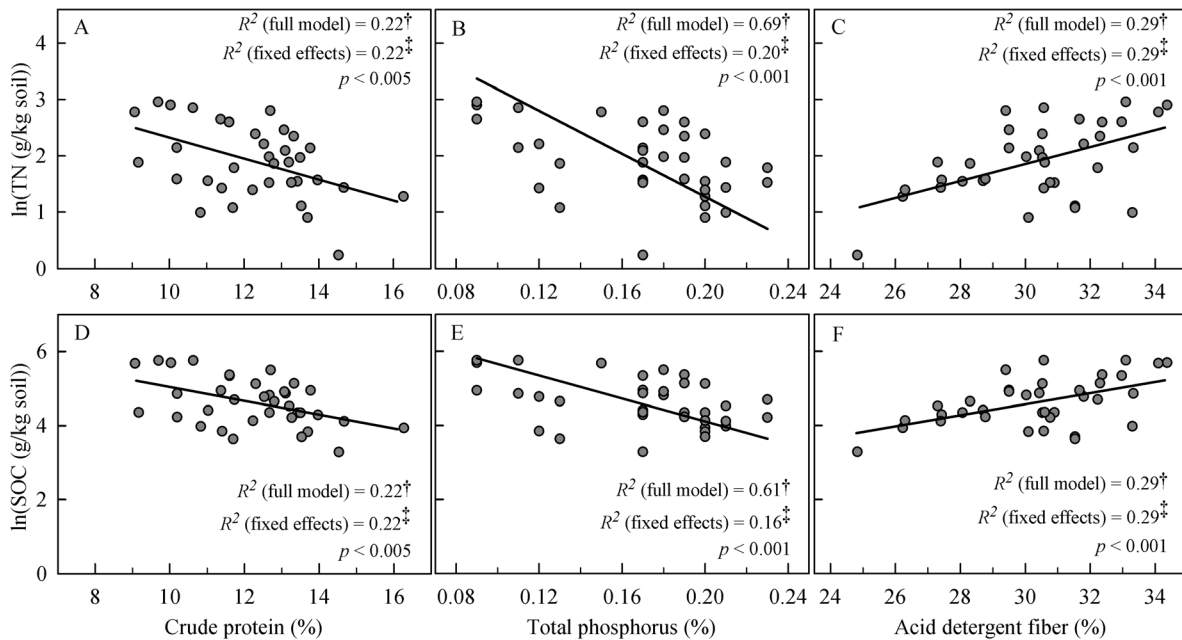


Fig. 7. Relationships between forage quality metrics and (A) total nitrogen (TN) and (B) total soil organic carbon (SOC). TN and SOC values are ln(50-cm depth-weighted averages). The p -values are from linear mixed effects model results (i.e., Wald test of fixed regression coefficient). A dagger (†) indicates pseudo- R^2 values calculated from linear regression between observed and predicted values with predictions based on fixed and random effects; a double dagger (‡) indicates pseudo- R^2 values calculated from linear regression between observed and predicted values with predictions based on fixed effects only (cf. Tate et al. 2003, Gabriel et al. 2010).

leading to the accumulation of organic materials (and formation of organic soil horizons)—giving rise to greater amounts of total C and N in these environments. The non-linear responses of SOC, TN, and SOM to patch hydrology (Fig. 6) suggest that C and N stocks may be fairly stable above a hydrologic threshold; below this critical threshold, wetland desiccation (e.g., following increased frequency and severity of drought) may lead to long-term losses in SOC, TN, and SOM stocks. Soil characteristics were also strongly correlated with herbaceous forage quality (Fig. 7)—and, in general, hydropedologic conditions (i.e., resulting from interactions between the pedosphere and hydrosphere) were significantly linked to herbaceous plant community characteristics (Fig. 9), owing to the clear hydrologic controls and interdependent plant-soil feedbacks across these wetland systems (Norton et al. 2011).

Our results suggest that these grazed, functional meadows were largely resilient to the observed gradient of grazing intensities (Fig. 8)—

which are broadly indicative of grazing intensities in the previous 5–10 years (Roche et al. 2012). The lack of livestock impact on meadow soils is not surprising given these soils are largely hydric, with high SOM contents across all patch types (Table 2). The high SOM contents likely dissipate force from cattle trampling. Moreover, soils at wetter sites were mainly composed of fibric and hemic materials (i.e., slightly and intermediately decomposed residues with some plant structural elements still present), which potentially enhances site resilience to hoof compaction. Studies in similar systems have also found that organic soils are generally resilient to grazing intensities associated with riparian conservation grazing strategies (Wheeler et al. 2002, George et al. 2011). In addition to the intrinsic resiliency of these organic soils, the hydrologic-soil-plant feedbacks within this system apparently deter cattle grazing at the wettest sites—providing a natural protection mechanism for carbon stocks in soils most susceptible to higher

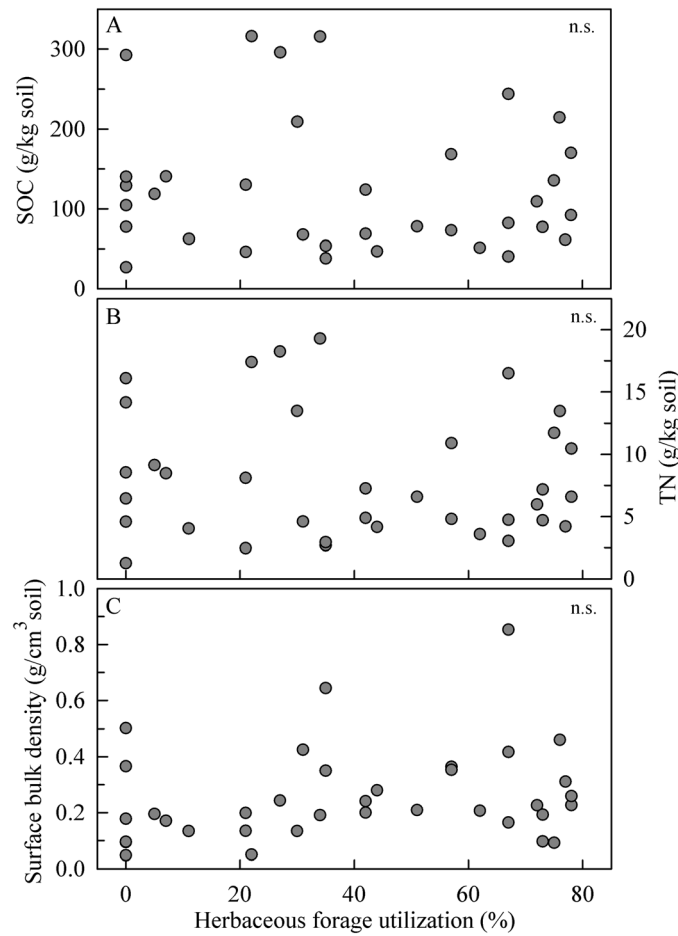


Fig. 8. Scatter plots of (A) total soil organic carbon (SOC; 50-cm depth-weighted averages), (B) total nitrogen (TN; 50-cm depth-weighted averages), and (C) surface bulk density by percent herbaceous utilization. The abbreviation “n.s.” indicates not significant.

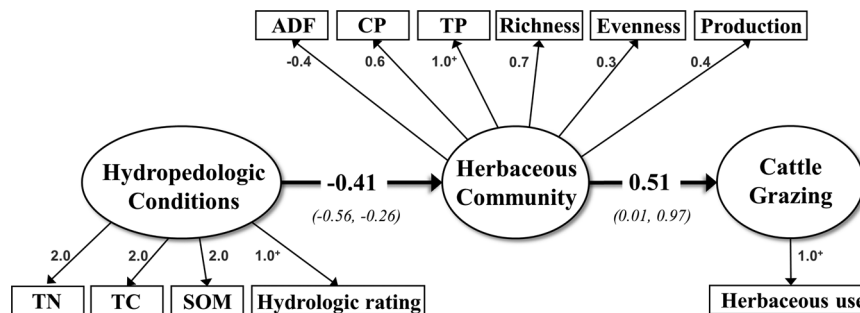


Fig. 9. Bayesian structural equation modeling results for relational pathways between hydropedologic conditions, herbaceous plant community, and cattle resource use patterns across meadow catenas. Ovals indicate latent variables, which are estimated by observable indicators, represented by boxes. A plus sign indicates a fixed value. Values in parentheses are 90% Bayesian credible intervals.

levels of disturbance and desiccation. We also found that mineral-dominated soils at the driest sites had thick, carbon-rich surface layers (Fig. 5 and Table 2), which apparently makes them resilient to the higher levels of livestock disturbance that they commonly experience (Fig. 3).

Hydrology was a critical driving factor of cattle foraging response, plant community attributes, and soil properties across these wetland systems. Changes in local hydrologic regimes could lead to an unraveling of the natural feedbacks and protection mechanisms that maintain meadow hydrologic functions and dependent ecosystem services (Fig. 1). For example, excessive grazing and hoof compaction can reduce groundcover, surface infiltration, and soil macropore space—negatively impacting water holding capacity, hydrologic function, and resistance to soil erosion (Trimble and Mendel 1995, Martin and Chambers 2002, Pietola et al. 2005, Loheide and Gorelick 2007). Excessive grazing can also trigger shifts in meadow plant communities from wetland to upland plant species (Kauffman and Krueger 1984, Cole et al. 2004, Kauffman et al. 2004), which could negatively impact herbaceous resources for both native and domestic grazers (Fig. 1). Therefore, utilization standards limiting grazing disturbances and adaptive grazing strategies controlling timing, intensity, and distribution of livestock grazing are critical in maintaining functional grazed systems and promoting win-win benefits for multiple ecosystem services, as observed in this study (e.g., positive relationships between species diversity, forage resource value, and cattle use) (Clary 1999, George et al. 2011, Freitas et al. 2014).

Projected climate change driven declines in long-term base flow conditions for the Sierra Nevada Range (Null et al. 2010) may lead to widespread desiccation of montane wetlands, which may have significant impacts for hydrologic function, herbaceous plant communities, and resulting grazing patterns. Wetland desiccation and increased drainage can also accelerate decomposition rates, making carbon stores vulnerable to decomposition and C loss (Schlesinger 1997). Changes in plant community composition and meadow hydrology may lead to greater overlap and potential conflicts in habitat use by cattle and sensitive amphibian species (Roche et

al. 2012). Given the central role of hydrology, managing land use activities to maintain and restore proper hydrologic functioning, as well as mitigating potential climate change impacts, are critical to sustaining multiple conservation and agricultural production outcomes across these wetland meadow ecosystems.

ACKNOWLEDGMENTS

We thank Neil McDougald and Dennis Dudley for sharing their invaluable expertise and advice. Ken Tate provided thoughtful insights and support. Jiayou Deng, Shannon Cler, Thomas Lushinsky, and Natalie Wegner provided field and lab assistance that made this project possible. This manuscript benefited from insightful comments from two anonymous reviewers.

LITERATURE CITED

- Acreman, M., and J. Holden. 2013. How wetlands affect floods. *Wetlands* 33:773–786.
- Allen-Diaz, B. H. 1991. Water table and plant species relationships in Sierra Nevada meadows. *American Midland Naturalist* 126:30–43.
- AOAC. 1997a. AOAC official method 973.18, fiber (acid detergent) and lignin in animal feed. Pages 28–29 *in* Official methods of analysis of AOAC International. ASA-SSA, Arlington, Virginia, USA.
- AOAC. 1997b. Chapter 12: AOAC official method 972.43, microchemical determination of carbon, hydrogen, and nitrogen, automated method. Pages 5–6 *in* Official methods of analysis of AOAC International. Sixteenth edition. ASA-SSA, Arlington, Virginia, USA.
- AOAC. 2006. AOAC official method 990.03, protein (crude) in animal feed, combustion method. Pages 30–31 *in* Official methods of analysis of AOAC International. ASA-SSA, Gaithersburg, Maryland, USA.
- Bailey, D. W., J. E. Gross, E. A. Laca, L. R. Rittenhouse, M. B. Coughenour, D. M. Swift, and P. L. Sims. 1996. Mechanisms that result in large herbivore grazing distribution patterns. *Journal of Range Management* 49:386–400.
- Belsky, A. J., A. Matzke, and S. Uselman. 1999. Survey of livestock influences on stream and riparian ecosystems in the western United States. *Journal of Soil and Water Conservation* 54:419–431.
- Blake, G. R., and K. H. Hartage, editors. 1986. Bulk density. Second edition. ASA-SSSA, Madison, Wisconsin, USA.
- Blank, R. R., T. Svejcar, and G. Riegel. 2006. Soil attributes in a Sierra Nevada riparian meadow as influenced by grazing. *Rangeland Ecology & Management* 59:321–329.

- Bollen, K. A. 1989. Structural equations with latent variables. John Wiley and Sons, New York, New York, USA.
- Bonham, C. D. 1989. Measurements for terrestrial vegetation. John Wiley and Sons, New York, New York, USA.
- Brunson, M. W., and B. S. Steel. 1996. Sources of variation in attitudes and beliefs about federal rangeland management. *Journal of Range Management* 49:69–75.
- Casanova, M. T., and M. A. Brock. 2000. How do depth, duration and frequency of flooding influence the establishment of wetland plant communities? *Plant Ecology* 147:237–250.
- Clary, W. P. 1999. Stream channel and vegetation responses to late spring cattle grazing. *Journal of Range Management* 52:218–227.
- Clary, W. P., and W. C. Leininger. 2000. Stubble height as a tool for management of riparian areas. *Journal of Range Management* 53:562–573.
- Clary, W. P., and B. F. Webster. 1990. Riparian grazing guidelines for the Intermountain region. *Rangelands* 12:209–212.
- Cole, D. N., J. W. van Wagtendonk, M. P. McClaran, P. E. Moore, and N. K. McDougald. 2004. Response of mountain meadows to grazing by recreational pack stock. *Journal of Range Management* 57:153–160.
- Congdon, P. 2003. Applied Bayesian modeling. Wiley, West Sussex, UK.
- Derner, J. D., D. D. Briske, and H. W. Polley. 2012. Tiller organization within the tussock grass *Schizachyrium scoparium*: a field assessment of competition-cooperation tradeoffs. *Botany* 90:669–677.
- Fleischner, T. L. 1994. Ecological costs of livestock grazing in western North America. *Conservation Biology* 8:629–644.
- Flenniken, M., R. R. McEldowney, W. C. Leininger, G. W. Frasier, and M. J. Trlica. 2001. Hydrologic responses of a montane riparian ecosystem following cattle use. *Journal of Range Management* 54:567–574.
- Freitas, M. F., L. M. Roche, D. W. Weixelman, and K. W. Tate. 2014. Montane meadow plant community response to livestock grazing. *Environmental Management* 54:301–308.
- Gabriel, D., S. M. Sait, J. A. Hodgson, U. Schmutz, W. E. Kunin, and T. G. Benton. 2010. Scale matters: The impact of organic farming on biodiversity at different spatial scales. *Ecology Letters* 13:858–869.
- Gelman, A., and J. Hill. 2007. Data analysis using regression and multilevel/hierarchical models. Cambridge University Press, Cambridge, UK.
- George, M., R. D. Jackson, C. S. Boyd, and K. W. Tate. 2011. A scientific assessment of the effectiveness of riparian management practices. Pages 213–252 in D. D. Briske, editor. Conservation benefits of rangeland practices: assessment, recommendations, and knowledge gaps. Allen Press, Lawrence, Kansas, USA.
- Grace, J. B. 2006. Structural equation modeling and natural systems. Cambridge University Press, Cambridge, UK.
- Hall, F. C., and L. Bryant. 1995. Herbaceous stubble height as a warning of impending cattle grazing damage to riparian areas. General Technical Report PNW-GTR-362. U.S. Forest Service Pacific Northwest Research Station, Portland, Oregon, USA.
- Hatfield, R. G., and G. LeBuhn. 2007. Patch and landscape factors shape community assemblage of bumble bees, *Bombus* spp. (Hymenoptera: Apidae), in montane meadows. *Biological Conservation* 139:150–158.
- Interagency. 1996. Utilization studies and residual measurements. Page 174 in Interagency technical reference BLM/RS/ST-96/004+1730. USDI Bureau of Land Management's National Applied Resources Science Center, Denver, Colorado, USA.
- Kauffman, J. B., and W. C. Krueger. 1984. Livestock impacts on riparian ecosystems and streamside management implications: a review. *Journal of Range Management* 37:430–438.
- Kauffman, J. B., A. S. Thorpe, and E. N. J. Brookshire. 2004. Livestock exclusion and belowground ecosystem responses in riparian meadows of Eastern Oregon. *Ecological Applications* 14:1671–1679.
- Kie, J. G., and B. B. Boroski. 1996. Cattle distribution, habitats, and diets in the Sierra Nevada of California. *Journal of Range Management* 49:482–488.
- Kluse, J. S., and B. H. Allen-Diaz. 2005. Importance of soil moisture and its interaction with competition and clipping for two montane meadow grasses. *Plant Ecology* 176:87–99.
- Kuhn, T. J., H. D. Safford, B. E. Jones, and K. W. Tate. 2011. Aspen (*Populus tremuloides*) stands and their contribution to plant diversity in a semiarid coniferous landscape. *Plant Ecology* 212:1451–1463.
- Lee, S. 2007. Structural equation modeling: A Bayesian approach. Wiley, West Sussex, UK.
- Loheide, S. P., R. S. Deitchman, D. J. Cooper, E. C. Wolf, C. T. Hammersmark, and J. D. Lundquist. 2009. A framework for understanding the hydroecology of impacted wet meadows in the Sierra Nevada and Cascade ranges, California, USA. *Hydrogeology Journal* 17:229–246.
- Loheide, S. P., and S. M. Gorelick. 2007. Riparian hydroecology: a coupled model of the observed interactions between groundwater flow and meadow vegetation patterning. *Water Resources Research* 43:1–16.
- Martin, D., and J. Chambers. 2002. Restoration of riparian meadows degraded by livestock grazing: Above and belowground responses. *Plant Ecology*

- 163:77–91.
- Matejkova, I., R. van Diggelen, and K. Prach. 2003. An attempt to restore a central European species-rich mountain grassland through grazing. *Applied Vegetation Science* 6:161–168.
- McCune, B., and J. B. Grace. 2002. Analysis of ecological communities. MjM Software, Gleneden Beach, Oregon, USA.
- McIlroy, S. K., and B. H. Allen-Diaz. 2012. Plant community distribution along water table and grazing gradients in montane meadows of the Sierra Nevada Range (California, USA). *Wetlands Ecology and Management* 20:287–296.
- Meyer, G. A., and P. N. Keliher. 1992. An overview of analysis by inductively coupled plasma-atomic emission spectrometry. Pages 473–516 in A. Montaser and D. W. Golightly, editors. *Inductively coupled plasmas in analytical atomic spectrometry*. VCH Publishers, New York, New York, USA.
- Middleton, B. A., B. Holsten, and R. van Diggelen. 2006. Biodiversity management of fens and fen meadows by grazing, cutting and burning. *Applied Vegetation Science* 9:307–316.
- Nelson, D. W., and L. E. Sommers. 1996. Total carbon, organic carbon, and organic matter. Pages 961–1010 in D. L. Sparks, J. M. Bartels, and J. M. Bigham, editors. *Methods of soil analysis, Part 3: Chemical methods*. ASA-SSSA, Madison, Wisconsin, USA.
- Norton, J. B., L. J. Jungst, U. Norton, H. R. Olsen, K. W. Tate, and W. R. Horwath. 2011. Soil carbon and nitrogen storage in upper montane riparian meadows. *Ecosystems* 14:1217–1231.
- Null, S. E., J. H. Viers, and J. F. Mount. 2010. Hydrologic response and watershed sensitivity to climate warming in California's Sierra Nevada. *PLoS ONE* 5:1–16.
- Pietola, L., R. Horn, and M. Yli-Halla. 2005. Effects of trampling by cattle on the hydraulic and mechanical properties of soil. *Soil & Tillage Research* 82:99–108.
- Pineiro, G., J. M. Paruelo, M. Oesterheld, and E. G. Jobbagy. 2010. Pathways of grazing effects on soil organic carbon and nitrogen. *Rangeland Ecology & Management* 63:109–119.
- Pinheiro, J. C., and D. M. Bates. 2000. Mixed-effects models. In *S and S-PLUS*. Springer-Verlag, New York, New York, USA.
- PRISM. 2014. PRISM Climate Group. Northwest Alliance for Computational Science & Engineering, Oregon State University.
- Rabe-Hesketh, S., and A. Skrondal. 2008. Multilevel and longitudinal modeling using Stata. Second edition. Stata Press, College Station, Texas, USA.
- Ratliff, R. 1985. Meadows in the Sierra Nevada of California: state of knowledge. General technical report PSW-GTR-84. U.S. Forest Service, Berkeley, California, USA.
- Roche, L. M., A. M. Latimer, D. J. Eastburn, and K. W. Tate. 2012. Cattle grazing and conservation of a meadow-dependent amphibian species in the Sierra Nevada. *PLoS ONE* 7:e35734.
- Rosenthal, G., J. Schrautzer, and C. Eichberg. 2012. Low-intensity grazing with domestic herbivores: a tool for maintaining and restoring plant diversity in temperate Europe. *Tuexenia* 32:167–205.
- Sah, R. N., and R. O. Miller. 1992. Spontaneous reaction for acid dissolution of biological tissues in closed vessels. *Analytical Chemistry* 64:230–233.
- Schlesinger, W. H. 1997. *Biogeochemistry: an analysis of global change*. Academic Press, San Diego, California, USA.
- Senft, R. L., M. B. Coughenour, D. W. Bailey, L. R. Rittenhouse, O. E. Sala, and D. M. Swift. 1987. Large herbivore foraging and ecological hierarchies. *BioScience* 37:789–799.
- Soder, K. J., A. J. Rook, M. A. Sanderson, and S. C. Goslee. 2007. Interaction of plant species diversity on grazing behavior and performance of livestock grazing temperate region pastures. *Crop Science* 47:416–425.
- Soil Survey Staff. 2006. *Keys to soil taxonomy*. USDA Natural Resources Conservation Service, Washington, D.C., USA.
- Spiegelhalter, D. J., N. G. Best, B. R. Carlin, and A. van der Linde. 2002. Bayesian measures of model complexity and fit. *Journal of the Royal Statistical Society Series B, Statistical Methodology* 64:583–616.
- Spiegelhalter, D., A. Thomas, N. Best, and D. Lunn. 2007. *OpenBUGS user manual*. Version 3.0.2. MRC Biostatistics Unit, Cambridge, UK.
- StataCorp. 2013. *Stata statistical software: release 13.0*. Stata Press, College Station, Texas, USA.
- Symstad, A. J., and J. L. Jonas. 2011. Incorporating biodiversity into rangeland health: plant species richness and diversity in Great Plains grasslands. *Rangeland Ecology & Management* 64:555–572.
- Tate, K. W., E. R. Atwill, N. K. McDougald, and M. R. George. 2003. Spatial and temporal patterns of cattle feces deposition on rangeland. *Journal of Range Management* 56:432–438.
- Thomas, A., B. O. Hara, U. Ligges, and S. Sturtz. 2006. Making BUGS open. *R News* 6:12–17.
- Thomas, G. W., editor. 1996. *Soil pH and soil acidity*. ASA-SSSA, Madison, Wisconsin, USA.
- Toledo, Z. O., and J. B. Kauffman. 2001. Root biomass in relation to channel morphology of headwater streams. *Journal of the American Water Resources Association* 37:1653–1663.
- Trimble, S. W., and A. C. Mendel. 1995. The cow as a geomorphic agent: A critical review. *Geomorphology* 13:233–253.
- Wallace, L. L., and K. A. Crosthwaite. 2005. The effect of fire spatial scale on Bison grazing intensity.

- Landscape Ecology 20:337–349.
- WallisDeVries, M. F., E. A. Laca, and M. W. Demment. 1998. From feeding station to patch: Scaling up food intake measurements in grazing cattle. *Applied Animal Behaviour Science* 60:301–315.
- WallisDeVries, M. F., E. A. Laca, and M. W. Demment. 1999. The importance of scale of patchiness for selectivity in grazing herbivores. *Oecologia* 121:355–363.
- Weiher, E., and P. Keddy. 1999. *Ecological assembly rules: Perspectives, advances, retreats*. Cambridge University Press, Cambridge, UK.
- Weiher, E., and P. A. Keddy. 1995. The assembly of experimental wetland plant-communities. *Oikos* 73:323–335.
- Wheeler, M. A., M. J. Trlica, G. W. Frasier, and J. D. Reeder. 2002. Seasonal grazing affects soil physical properties of a montane riparian community. *Journal of Range Management* 55:49–56.
- Wood, S. H. 1975. *Holocene stratigraphy and chronology of mountain meadows, Sierra Nevada, California*. Page 180. *Earth Resources Monograph 4*. U.S. Forest Service Region 5, San Francisco, California, USA.